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Integrated population models poorly estimate the demographic contribution of immigration

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Abstract

1. Estimating the contribution of demographic parameters to changes in population growth is essential for understanding why populations fluctuate. Integrated population models (IPMs) offer a possibility to estimate the contributions of additional demographic parameters, for which no data have been explicitly collected—typically immigration. Such parameters are often subsequently highlighted as important drivers of population growth. Yet, accuracy in estimating their temporal variation, and consequently their contribution to changes in population growth rate, has not been investigated.
2. To quantify the magnitude and cause of potential biases when estimating the contribution of immigration using IPMs, we simulated data (using northern wheatear *Oenanthe oenanthe* population estimates) from controlled scenarios to examine potential biases and how they depend on IPM parameterization, formulation of priors, the level of temporal variation in immigration and sample size. We also used empirical data on populations with known rates of immigration: Soay sheep *Ovis aries* and Mauritius kestrel *Falco punctatus* with zero immigration and grey wolf *Canis lupus* in Scandinavia with near-zero immigration.
3. IPMs strongly overestimated the contribution of immigration to changes in population growth in scenarios when immigration was simulated with zero temporal variation (proportion of variance attributed to immigration = 63% for the more constrained formulation and real sample size) and in the wild populations, where the true number of immigrants was zero or near-zero (kestrel 19.1%–98.2%, sheep

4.2%–36.1% and wolf 84.0%–99.2%). Although the estimation of the contribution of immigration in the simulation study became more accurate with increasing temporal variation and sample size, it was often not possible to distinguish between an accurate estimation from data with high temporal variation versus an overestimation from data with low temporal variation. Unrealistically, large sample sizes may be required to estimate the contribution of immigration well.

4. To minimize the risk of overestimating the contribution of immigration (or any additional parameter) in IPMs, we recommend to: (a) look for evidence of variation in immigration before investigating its contribution to population growth, (b) simulate and model data for comparison to the real data and (c) use explicit data on immigration when possible.

KEYWORDS

immigration, integrated population models, parameter estimation, temporal variation, transient Life Table Response Experiment contribution

1 | INTRODUCTION

Quantifying the relative contribution of demographic parameters to population growth is essential for understanding the processes influencing population dynamics (Caswell, 2000; Coulson et al., 2005; Koons et al., 2016). This is important in population research, where identifying these relationships not only can help to predict the effectiveness of targeted conservation measures on population growth but also to provide information about the spatial scale at which conservation management should be taken (Schaub et al., 2012; Zipkin & Saunders, 2018). For example, if local reproduction is a strong contributor to population growth, this suggests that measures supporting reproduction at the local scale may be an effective strategy at managing the population, while a strong contribution of immigration would instead suggest that supportive measures should be undertaken at a larger spatial scale. However, acquiring data on all demographic parameters and their temporal variation is often challenging. In particular, the measures of immigration are often limited or absent from datasets (Abadi et al., 2010). For this reason, modelling approaches such as integrated population models (IPMs) have been developed that use other demographic data to estimate the missing demographic parameters and their contribution to population growth rates (Abadi et al., 2010; Schaub & Fletcher, 2015; Schaub et al., 2013).

IPMs combine data on demographic rates with data on population size to allow: (a) an estimate of changes in both demographic rates and population growth rate in a joint analysis, and in some cases (b) to estimate *additional* demographic parameters (Riecke et al., 2019) for which no data have been explicitly collected by integrating information from available data on other parameters and population growth (Kéry & Schaub, 2011; Schaub & Abadi, 2011). Therefore, IPMs offer the exciting possibility to investigate how changes in a demographic parameter are associated with changes in population growth rate, even in cases where no explicit data on this parameter are available (Millon et al., 2019). Hence, a rapidly increasing number of recent studies have used IPMs to estimate the contribution of such additional parameters, typically immigration (e.g. Schaub et al., 2012; Taylor et al., 2018; Weegman et al., 2017), but also productivity or breeding success when populations are assumed to be closed to immigration (Baillie et al., 2009; e.g. Besbeas et al., 2002; Nuijten et al., 2020).

However, since no explicit data are used, estimating the contribution of an additional demographic parameter such as immigration rate must be based on particular modelling assumptions. It has been shown that estimation of the mean immigration rate can be sensitive to the parametrization and priors chosen (Schaub & Fletcher, 2015), and that systematic bias in the estimation of other parameters results in biased estimation of immigration (Riecke et al., 2019). Similarly, the estimation of the temporal variation of immigration (and consequently its contribution to temporal variation in population growth) could also depend on how this variation is parameterized and on the presence of any bias in the temporal variation of the other parameters. Indeed, any residual temporal variation of the other demographic parameters (e.g. temporal random noise in detection probability, density dependence, temporal trends), if not explicitly considered in the models, will likely result in bias of the contribution of immigration to changes in population growth. Given this, caution is needed when interpreting the findings of the many studies that show immigration has the strongest contribution to changes in population growth rate (70% of 44 immigration parameters estimated from 23 studies compiled in Table 1). Because it is the residual variation that is used to estimate 'missing' parameters like immigration (together with the variance of the observation model), the model parameterization is likely to influence these estimates (Paquet et al., 2019; Saunders et al., 2018; Schaub et al., 2013). Despite this, the vast majority of IPM studies interpret

TABLE 1 Summary of studies that have used IPMs to estimate the contribution of immigration to population growth rates

Study	Species	Model details	Est. mean immigr.	Estimated contribution	Method	>95% certainty	Strongest contribution	Biological conclusions	Conservation conclusions	Bias discussed
1	*Upupa epops*	P, R	0.28	0.57 (−0.35 to 0.88)	cor	N	N	Y	Y	N
	Jynx torquilla		0.25	0.86 (−0.07 to 0.94)		N	N			
2	*Lanius collurio*	P, R	0.56	0.62 (0.37 to 0.81)	cor	Y	Y	Y	Y	N
3	*Strix occidentalis*	P, R	0.1	0.58 (NA)	cor	Y	Y	Y	Y	N
4	*Sterna hirundo*	U, F	0.16	0.93 (NA)	cor	Y	Y	Y	N	N
5	*Hirundo rustica*	P, R	0.47	0.55 (NA)	contr	Y	Y	Y	N	Y
6	*Anser albifrons*	P, F	0.17	0.81 (0.72 to 0.87)	cor	Y	Y	Y	N	N
7	*Passerculus sandwichensis*	P, R	0.29	0.46 (0.27 to 0.63)	reg	Y	Y	Y	N	N
8	*Hylocichla mustelina*	P, R	0.19	0.12 (0.05 to 0.2)	contr	Y	N	Y	N	N
			0.35	0.51 (0.35 to 0.65)		Y	Y			
			0.23	0.2 (0.08 to 0.34)		Y	N			
			0.26	0.24 (0.14 to 0.35)		Y	N			
			0.31	0.42 (0.31 to 0.54)		Y	Y			
			0.31	0.48 (0.38 to 0.59)		Y	Y			
			0.32	0.48 (0.35 to 0.6)		Y	Y			
			0.29	0.36 (0.26 to 0.47)		Y	N			
			0.31	0.36 (0.24 to 0.48)		Y	N			
			0.42	0.41 (0.24 to 0.59)		Y	N			
			0.51	0.43 (0.24 to 0.62)		Y	N			
			0.54	0.32 (0.16 to 0.48)		Y	N			
9	*Pteromys volans*	U, F	0.47	0.96 (0.8 to 0.99)	cor	Y	Y	Y	Y	N
			0.27	0.95 (0.84 to 0.99)		Y	Y			
10	*Tachycineta bicolor*	P, R	0.26	0.79 (0.37 to 0.91)	cor	Y	Y	Y	N	N
			0.23	0.77 (0.28 to 0.88)		Y	Y			
			0.43	0.9 (0.65 to 0.95)		Y	Y			
11	*Setophaga ruticilla*	P, R	0.57	0.16 (NA)	cor	N	N	Y	N	N
12	*Platalea leucorodia*	P, R	0.36	0.84 (0.53 to 0.93)	Cor	Y	Y	Y	N	N
13	*Tachycineta bicolor*	P, R	0.35	0.7 (NA)	contr	Y	Y	Y	N	Y
14	*Charadrius melodus*	P, R	0.09	0.31 (−0.15 to 0.77)	cor	N	N	N	N	Y
15	*Falco tinnunculus*	N, R	−0.38	0.37 (NA)	contr	N	Y	N	N	Y
16	*Oenanthe oenanthe*	U, R	0.44	0.82 (NA)	contr	Y	Y	N	N	Y

(Continues)

TABLE 1 (Continued)

Study	Species	Model details	Est. mean immigr.	Estimated contribution	Method	>95% certainty	Strongest contribution	Biological conclusions	Conservation conclusions	Bias discussed
17	*Vanellus vanellus*	NA	NA	0.04 (NA)	NA	NA	N	Y	N	N
18	*Cardellina pusilla*	N+, F	NA	0.82 (NA)	contr	Y	Y	N	N	Y
				0.65 (NA)		Y	Y			
				0.64 (NA)		Y	Y			
19	*Upupa epops*	P, R	0.27	0.24 (NA)	contr	NA	N	N	N	N
20	*Lanius senator*	P, R	0.5	0.83 (NA)	contr	Y	Y	Y	Y	Y
21	*Charadrius melodus*	P, F	0.47	0.92 (0.22 to 0.98)	cor	Y	Y	Y	Y	Y
22	*Falco sparverius*	U, F	0.21	NA	cor	Y	Y	Y	Y	N
			0.21	NA		Y	Y			
			0.15	NA		Y	Y			
			0.2	NA		N	Y			
23	*Jynx torquilla*	P, F	NA	0.58 (NA)	contr	Y	Y	Y	N	N
			NA	0.87 (NA)		Y	Y			

Note: Species: The scientific name of the species studied.

Model details: likelihood (Pois = Poisson, N = Normal, *N+* = truncated Normal and U = Uniform prior), and how immigration was estimated (F = fixed, R = random).

Est mean immigr: estimated mean immigration rate.

Estimated contribution: estimated contribution (mean and 95% CIs) of immigration to population growth as value of the correlation, contribution (i.e. % of variation in population growth explained by immigration) or regression coefficient (see column 'Immigr method').

Method: method used to calculate the estimated contribution of immigration: cor = correlation coefficient, contr = LTRE contribution and reg = regression coefficient.

>95% certainty: whether the 95% CIs of the estimated contribution of immigration overlapped zero.

Strongest contribution: whether immigration was estimated to be the strongest contributor to variation in growth rate compared with the other demographic parameters.

Biological conclusions: whether biological conclusions were drawn from the contribution of immigration.

Conservation conclusions: whether recommendations or management decisions were suggested based on the contribution of immigration.

Bias discussed: whether potential modelling biases that could explain the contribution of immigration were discussed.

References (numbers relate to those in the column 'Study').

1. Schaub et al. (2012). The demographic drivers of local population dynamics in two rare migratory birds. *Oecologia*.
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4. Szostek et al. (2015). Immigrants are attracted by local pre-breeders and recruits in a seabird colony. *Journal of Animal Ecology*.
5. Schaub et al. (2015). Differential contribution of demographic rate synchrony to population synchrony in barn swallows. *Journal of Animal Ecology*.
6. Weegman et al. (2016). Integrated population modelling reveals a perceived source to be a cryptic sink. *Journal of Animal Ecology*.
7. Woodworth et al. (2017). Winter temperatures limit population growth rate of a migratory songbird. *Nature Communications*.
8. Clark et al. (2017). Spatial and temporal drivers of avian population dynamics across the annual cycle. *Ecology*.
9. Brommer et al. (2017). Immigration ensures population survival in the Siberian flying squirrel. *Ecology and Evolution*.
10. Weegman et al. (2017). Integrated population models reveal local weather conditions are the key drivers of population dynamics in an aerial insectivore. *Oecologia*.

(Continues)

TABLE 1 (Continued)

11. Wilson et al. (2017). Density-dependent immigration promotes population stability in a long-distance migratory bird. *Population Ecology*.
12. Tenan et al. (2017). Conspecific and not performance-based attraction on immigrants drives colony growth in a waterbird. *Journal of Animal Ecology*.
13. Taylor et al. (2018). Demographic drivers of collapse in an island population of Tree Swallows. *The Condor*.
14. Saunders et al. (2018). Evaluating population viability and efficacy of conservation management using integrated population models. *Journal of Applied Ecology*.
15. Fay et al. (2019). Integrated population model reveals that kestrels breeding in nest boxes operate as a source population. *Ecography*.
16. Paquet et al. (2019). Quantifying the links between land use and population growth rate in a declining farmland bird. *Ecology and Evolution*.
17. Plard et al. (2019). Low productivity and unsuitable management drive the decline of central European lapwing populations. *Animal Conservation*.
18. Saracco and Rubenstein. (2020). Integrating broad-scale data to assess demographic and climatic contributions to population change in a declining songbird. *Ecology and Evolution*.
19. Plard et al. (2020). Disentangling the spatial and temporal causes of decline in a bird population. *Ecology and Evolution*.
20. Schaub and Ullrich. (2020). A drop in immigration results in the extinction of a local woodchat shrike population. *Animal Conservation*.
21. Robinson et al. (2020). Piping Plover population increase after Hurricane Sandy mediated by immigration and reproductive output. *The Condor*.
22. McClure et al. (2020). Demography of a widespread raptor across disparate regions. *Ibis*.
23. Tenan et al. (2020). Decomposing fecundity and evaluating demographic influence of multiple broods in a migratory bird. *Journal of Animal Ecology*.

this contribution exclusively as immigration (Table 1). Thus, there is an obvious need to estimate what proportion of the estimated contribution of immigration is truly due to immigration and not to some other component of the residual variation.

Here we use a combination of simulated and empirical data to assess the accuracy of IPMs in estimating immigration as a driver of temporal changes in population growth when immigration is not measured directly. First, we used simulation scenarios to confirm the existence and examine the cause of bias in estimating immigration within the IPM framework. Using 'perfect datasets' simulated with known immigration, we investigate whether IPM parametrization, specification of priors and the method of estimating population growth contribution result in biased estimates of the demographic contribution of immigration. Demographic parameter values other than immigration were based on estimates from an open population of northern wheatear, *Oenanthe oenanthe*, near Uppsala, Sweden. The simulation study allows us to quantify the bias in the estimation of the temporal variation of immigration and its contribution to population growth under various scenarios. Second, we use long-term data from real populations with known immigration, in order to compare the IPM-estimated contribution of immigration versus the known true contribution of immigration. More specifically, we used data from populations that are either closed to immigration (Soay sheep *Ovis aries* on the island of Hirta and Mauritius kestrels *Falco punctatus*) or where the number of immigrants is very small and known (grey wolf *Canis lupus* population of Scandinavia).

2 | MATERIALS AND METHODS

2.1 | Simulation study

To assess how accurate IPMs are at estimating the temporal variation and contribution of immigration to changes in population growth rate, we simulated data using known parameter values for fecundity, apparent survival (i.e. accounting for both emigration and mortality), population size and immigration. We then applied IPMs to the simulated data and compared modelled parameter estimates to the known values (see Appendix 1 for the scripts used to simulate data and to fit IPMs to simulated data). We simulated a series of datasets (and their underlying time-varying demographic parameters) using the structure of IPMs adapted from the real-data IPM example in Kéry and Schaub (2011) with time varying (random) vital rates, demographic stochasticity accounted for using Poisson and Binomial distributions and a Poisson distribution for the observation model of the count data. We simulated the number of immigrants rather than an immigration rate as it has been suggested to better estimate immigration, particularly in small populations, whereas modelling immigration rate may lead to unrealistically high estimates due to its dependency to population size (Schaub & Fletcher, 2015; Zipkin & Saunders, 2018). To obtain realistic parameter values for the simulations, we fitted the same IPM structure to a dataset from a northern wheatear population of central Sweden that is open to immigration

(Paquet et al., 2020). For all parameters except the number of immigrants (for which further details are given below), we used the posterior medians from this fit in the simulation (see Appendix 1 for parameter values).

2.1.1 | Scenarios

To quantify the bias in the estimation of the temporal variation of immigration and its contribution, we simulated six scenarios that resulted from the combination of using three levels of temporal variation in the number of immigrants (no, moderate or strong) and two levels of sample size. In the no variation in immigration scenario, we kept the number of immigrants fixed at the median of its value as estimated from the wheatear data ($N_{imm,t} = e^{\mu_{imm}} = 32$, which corresponds to 39% of the initial population size). For the moderate and strong variation in immigration scenarios, we fixed the temporal standard deviation of the number of immigrants (on the log scale), hereafter σ_{imm}, to either 0.2 (simulating moderate temporal variation) or 0.4 (simulating strong temporal variation).

$$N_{imm,t} \sim \text{Poisson}\left(e^{(\mu_{imm}+\varepsilon_{imm,t})}\right),$$

$$\varepsilon_{imm,t} \sim \text{Normal}(0, \sigma_{imm}).$$

To understand how sensitive the estimates of σ_{imm} are to the amount of data available, we simulated 24 years' datasets of 'normal' sample size (the same sample sizes per year as in the real wheatear dataset, see Appendix 1 for sizes of simulated datasets) or 'large' sample sizes (sample sizes per year 10 times larger than the wheatear data; with the initial population size and mean number of immigrants also 10 times bigger).

2.2 | Estimating time-varying immigration and its contribution to population growth rate

To estimate temporal variation in the number of immigrants, we fitted the two most typically used formulations on each dataset (Table 1). In the first, most widely used type of IPM (hereafter IPM_{Pois}), the number of immigrants is strictly positive and allowed to vary around a mean value according to a Poisson log-normal distribution (e.g. Schaub et al., 2012, 2013; Taylor et al., 2018). In the second type of IPM (hereafter $IPM_{NoConst}$), the number of immigrants is a fixed parameter estimated independently for each year (Brommer et al., 2017; e.g. Szostek et al., 2014), without constraining the number of immigrants to be positive, nor to vary randomly around a mean.

We estimated the contribution of immigration to changes in population growth rate using the two most common methods. First, we calculated the correlation coefficient between the annual number of immigrants and the annual population growth rates for each posterior sample, as well as the proportion of positive coefficients (Schaub et al., 2012). Second, we computed recently developed transient Life Table Response Experiment (LTRE) contributions for immigration rate (Koons et al., 2016, 2017; Taylor et al., 2018). This method has the advantage of summing into a meaningful quantity, which should approximate the variation in population growth rate and therefore allows an estimate of the proportion of variation in annual population growth that is explained by the variation in immigration rate (Paquet et al., 2019; Taylor et al., 2018). Given the limitations of the ad hoc correlation approach, notably for comparisons among populations (Koons et al., 2017), we only present results from the LTRE contributions in the main text and refer to results from the correlation approach in Figures S3 and S6.

For each of the six scenarios, we simulated 100 datasets. For each of the 600 datasets, we fitted the two above-mentioned types of Bayesian IPMs (IPM_{Pois} and $IPM_{NoConst}$, see Appendix 1). For each IPM, we obtained posterior distributions from three independent MCMC chains after an adaptation period of 5,000 iterations, a burn in of 1,000 sampling every 30th iteration for 30,000 iterations. We used vague priors and true parameter values of the simulated datasets as initial values except for σ_{imm} which was initially set to 0.02 for cases where the true number of immigrants did not vary.

The correlations between the yearly number of immigrants and the growth rate and the LTRE contribution of immigration rate were computed from the posterior samples, and their true values were calculated for each of the simulated datasets for comparison. We looked at the correlations with the number of immigrants rather than immigration rates (e.g. Saunders et al., 2018), whereas contribution had to be calculated for immigration rate. Note that the true LTRE contribution of immigration rate is positive even when the number of immigrants is fixed because population size, and hence immigration rate, still varies when the number of immigrants is fixed.

2.3 | Case studies on three real populations

To assess how accurate IPMs are at estimating the temporal variation of immigration and its contribution in real populations, we compare estimated and true contribution of immigration using long-term data from real populations with known rates of immigration (see Appendix 2 for details on sample sizes, methods and references describing data collection). We built Bayesian IPMs with time varying (random) vital rates. We modelled female breeders only, assuming females are the limiting sex (Rankin & Kokko, 2007). A detailed description of the models is provided in Appendix 3.

For each IPM, we obtained posterior distributions from three independent MCMC chains. Details on prior distribution, initial values, number of iterations, convergence assessment and posterior predictive checks can be found in Appendix 4. All simulations and estimations of posterior distributions were performed using JAGS, version 4.2.0 (Plummer, 2003, 2015) run using the rjags package (Plummer, 2013) in Program R, version 3.3.1 (R Core Team, 2019). R

code to compute LTRE contributions and correlations is provided in Appendix 5.

3 | RESULTS

3.1 | Simulation study

Both IPM parameterizations satisfactorily predicted the mean (i.e. 32 and 320 for both sample sizes) and annual number of immigrants in all scenarios (see Figure S1 for illustration on one of the 100 datasets in each scenario). Nevertheless, IPMs overestimated the LTRE contribution of immigration (Figure 1; Figure S2, panels A and D) as well as the correlation between the estimated number of immigrants and population growth rate (Figure S3) for most of the simulations where the number of immigrants did not vary (Table S1; Figure 2). This is because the variation in the number of immigrants was overestimated, due to estimation uncertainty combined with the fact that the standard deviation is constrained to be positive (Figure 3).

When the simulated number of immigrants varied moderately or strongly over time, the IPM_{Pois} gave unbiased estimates of the variance in the number of immigrants (Figure 3) and consequently the contributions of immigration rate to changes in population growth rate (Figure 2). However, the estimated contributions were not clearly different from what would have been estimated in absence of variation in the number of immigrants (Figure 1: 95% CrI for IPM estimates in panel B or C [with temporal variation in immigration] largely overlap with those in panel A [no variation]). The differences were more pronounced, although still unclear, when the sample sizes were increased 10-fold (Figure 1d–f).

The $IPM_{NoConst}$ poorly estimated the LTRE contributions of immigration rate in all cases (Figure 2).

3.2 | Case studies

For all case studies, estimated numbers of immigrants were small relative to population size, and 95% credible intervals almost always included zero (Figure S4). Their temporal variation (estimated with the IPM_{Pois} parameterization) was also low and did not clearly deviate from zero (Figure S5). The kestrel and the sheep populations are closed to immigration, and for the wolf population, where immigration did occur twice, the posterior contribution of the true immigration rate was close to zero -3.46×10^{-5} (95% CrI: $-0.16.8 \times 10^{-5}$, 6.83×10^{-5}). Despite this, for all three populations, estimates of the LTRE contribution of immigration were positive for most posterior samples for the IPM_{Pois} formulation and strong for *all* posterior samples for the $IPM_{NoConst}$ formulation (Figure 4). Computing correlations gave similar results (Figure S6). When using the IPM_{Pois} formulation, LTRE analyses suggest that immigration explained on average 19.1% of the variation in population growth rate for the kestrel population, 4.2% for the sheep population and 84.0% for the wolf population (Figure 4, calculated as: $\text{mean}(\text{Contrib}_{Imm})/\text{mean}(\text{Contrib}_{Imm} + \text{Contrib}_{\text{Other demographic rates}})$). The LTRE contribution of immigration increased dramatically when using the $IPM_{NoConst}$ formulation, representing then 98.2% of the variation in population growth rate for the kestrel population, 36.1% for the sheep population and 99.2% for the wolf population (Figure 4).

4 | DISCUSSION

Using both simulations and real case studies, we show that IPMs can strongly overestimate the contribution of immigration to changes in population growth rate. This happened when immigration was simulated with zero temporal variation and in our case studies where immigration was known to be zero or negligible. The strength of this overestimation varied with how immigration was formulated and with sample size. The estimation of the contribution of immigration to variation in growth rate was more accurate when the true (simulated) variation in the number of immigrants was substantial (i.e. $\sigma_{imm} = 0.2$ or 0.4 on the log scale). However, despite this, it was still often not distinguishable from what was estimated when immigration did not vary. Below, we discuss the implications of these results and provide guidelines for more informed inference when estimating the importance of immigration (or any demographic parameter informed by little or no data) for population dynamics using IPMs.

Although previous empirical work has acknowledged the possibility for bias when estimating the contribution of immigration, for example due to spatial mismatch, lack of fit or unmodelled temporal variation in other parameters (Paquet et al., 2019; Saunders et al., 2018; Schaub et al., 2013), our simulation study shows that the contribution of immigration can be strongly overestimated, even in absence of any such biases. We found that in absence of variation in the number of immigrants and with a realistic sample size, the estimated variation in the number of immigrants was substantial (Figure 3; Figure S1a) and immigration rate was the demographic parameter contributing the most to changes in population growth rate (LTRE contribution representing 63% (95% CrI 30–95) of the total variation for the IPM_{Pois} parameterization, Figure S2). We found that such bias is particularly strong when using the least constrained formulation of immigration $IPM_{NoConst}$ for both the simulation study and the case studies. This is likely due to the uniform priors used to model the number of immigrants independently each year, which induce spurious temporal variation because of the high uncertainty in estimating yearly immigration. Although more rarely used, such formulation has been recommended instead of the IPM_{Pois} formulation to estimate the *mean* number of immigrants in cases where it is expected to be small (as for our case studies), because it allows negative values (Schaub & Fletcher, 2015), unlike the IPM_{Pois} formulation. While it does perform well in estimating the *mean* number of immigrants, we show that it performs poorly in estimating their temporal *variation*. A compromise to better estimate both the mean and temporal variation of immigration in cases where immigration is low could be to use a Normal likelihood for immigration rate as it allows for negative values (cf. $IPM_{NoConst}$) while having constant mean and

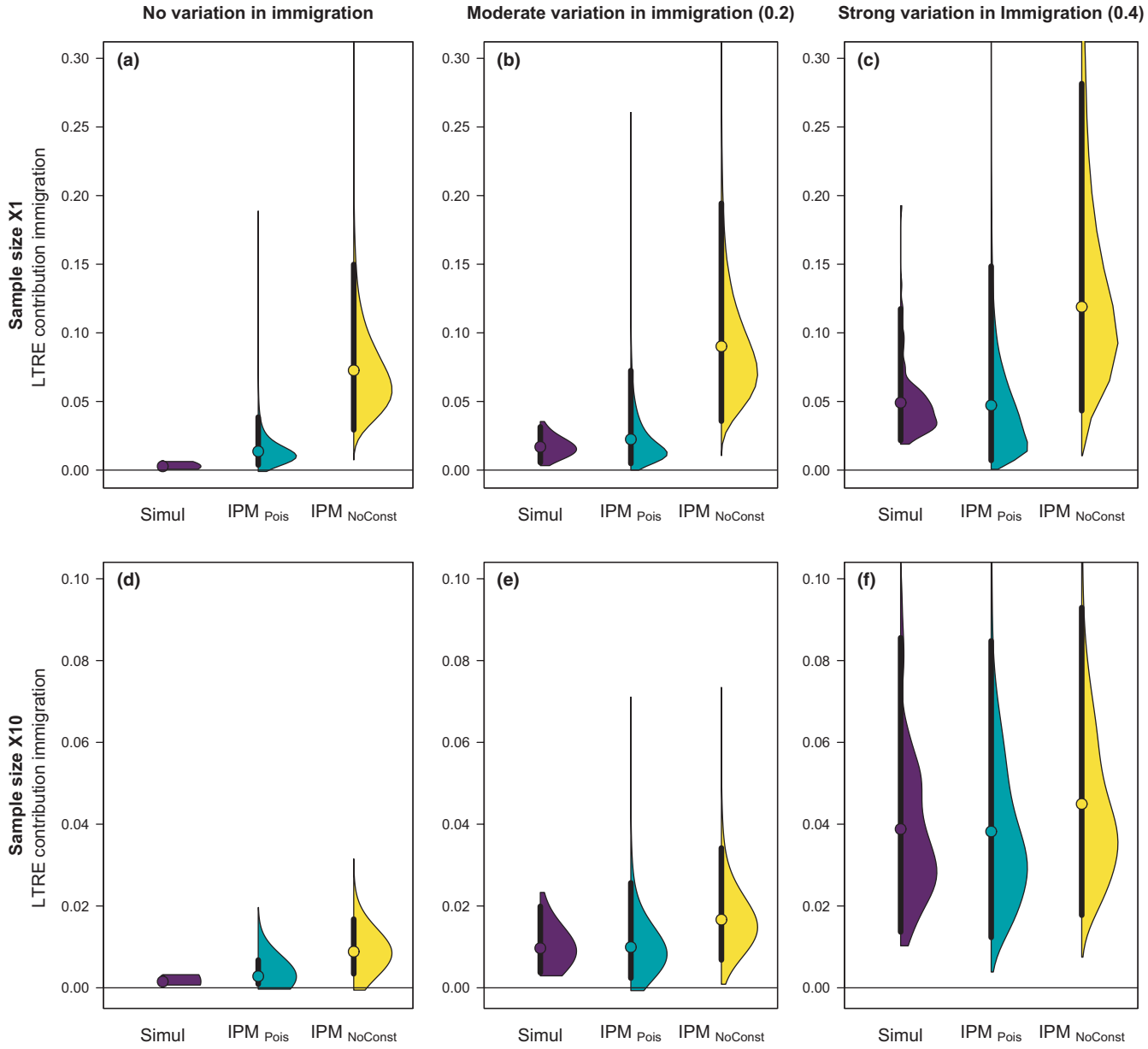

FIGURE 1 LTRE contribution of immigration rate to variance in population growth rate for the three simulated level of variation in the number of immigrants (a & d = no variation; b & e = moderate variation; c & f = strong variation) for both sample sizes (upper panels [a–c] for the original sample size and lower panels [d–f] for the 10-fold sample sizes). Simul represents the distribution of the 100 true values of the simulated datasets, and IPM_{Pois} and $IPM_{NoConst}$ represent the distribution of the combined posteriors for the contributions estimated with each IPM parameterization. In the IPM_{Pois} parameterization, the number of immigrants is positive with random temporal variation according to a Poisson log-normal distribution. For $IPM_{NoConst}$, the number of immigrants is estimated independently for each year. Dots show the posterior means, and lines show the 95% intervals for the combined posterior mass across simulations. Proportions of variation in growth rate explained by LTRE contribution of immigration are presented in Figure S2

temporal variance (cf. IPM_{Pois}; e.g. Fay et al., 2019). Nevertheless, using such a formulation would still presumably provide an overestimated contribution of immigration, as we found when using the IPM_{Pois} formulation. This is because the temporal variance parameters are constrained to be positive and therefore uncertainty around a true variance of zero leads to the occurrence of positive (not negative) posterior values (see Figure 3).

In simulations where immigration varied substantially, IPMs provided good estimates of temporal variation in immigration, and consequently good estimates of their contribution to changes in population growth. However, the estimated contributions may be largely indistinguishable from what would be expected if immigration would not vary (and hence not contribute at all to variation in population growth; Figure 1). Only very high variation in immigration and/or huge sample sizes would lead to estimates precise enough to distinguish the temporal variation and contribution of immigration from what would be expected in the absence of variation.

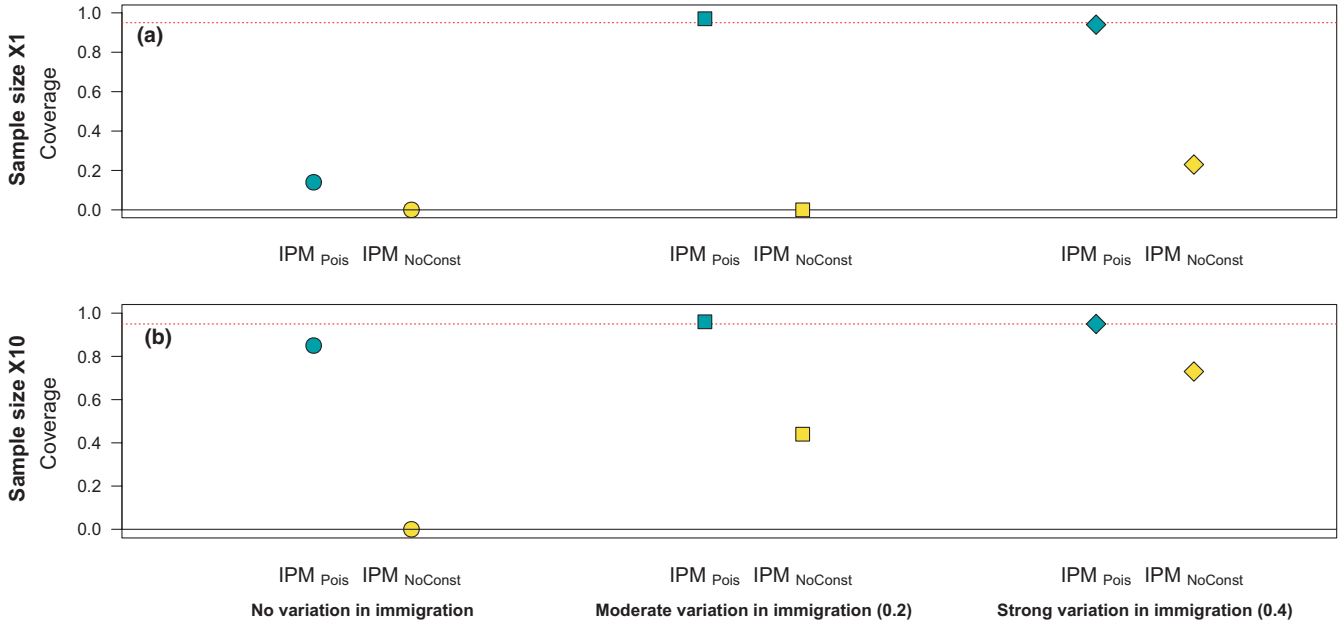

FIGURE 2 Coverages (= proportion of simulations where 95% CrI of estimated parameter includes the true parameter value) for LTRE contributions of immigration estimated under each simulated scenario (panel a = original sample size; panel b = 10-fold sample size). Green points represent the IPM_{Pois} parameterization and yellow points represent the $IPM_{NoConst}$ parameterization. The red dotted line indicates a coverage of 95%

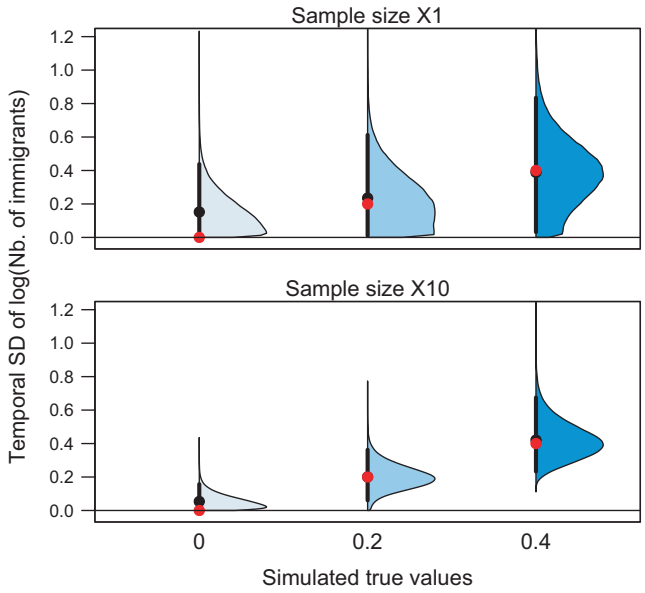

FIGURE 3 Temporal standard deviation in number of immigrants (on the log scale) estimated with the IPM_{Pois} parameterization for each true level of variation (i.e. 0, 0.2 and 0.4) and for both sample sizes. Violin plots show the distribution of the combined posteriors from all 100 simulated datasets. Red dots show true values, black dots show the means and bold lines show the 95% intervals for the combined posterior mass across simulations

Similar to results from the simulations, our case studies on the three wild populations with known immigration show that the contribution of immigration was overestimated for most of the posterior samples and most dramatically when using the least constrained formulation of immigration ($IPM_{NoConst}$, Figure 4). Such bias could be driven by many additional factors, including temporal variation in the observation process of the count data, any non-random temporal variation of the other demographic parameters that would not be explicitly considered in the model (Paquet et al., 2019) or a mismatch of the spatial scale used to estimate the different components of the models (Millon et al., 2019). Knowledge of the biology for each study population is therefore important and needs to be considered explicitly within the population model in order to minimize bias in the estimation of the contribution of *additional* parameters such as immigration.

It is important to note that such biased estimation of temporal variation likely applies to any *additional* parameter (estimated indirectly by integrating information from other parameters, Riecke et al., 2019), and, potentially to a lesser extent, any model parameter when there is uncertainty around the estimation of temporal variation, and the shape of its posterior distribution shows no clear deviation from zero. Therefore, the issues raised in this study should be carefully considered when estimating the temporal contribution of any parameter and when comparing the contribution of parameters informed by largely differing amounts of data.

What can be done in order to get better inference on the temporal contribution of immigration, or any other parameter, to population growth when using IPMs? We recommend to first look for evidence of variation before investigating its contribution to population growth. This can be done by evaluating the shape of the posterior distribution of its variance and assessing whether its peak clearly differs from zero (Figure 3). Although computationally more time-consuming, a second recommendation is to proceed as we did in our simulation study. That is, simulate datasets of the same size

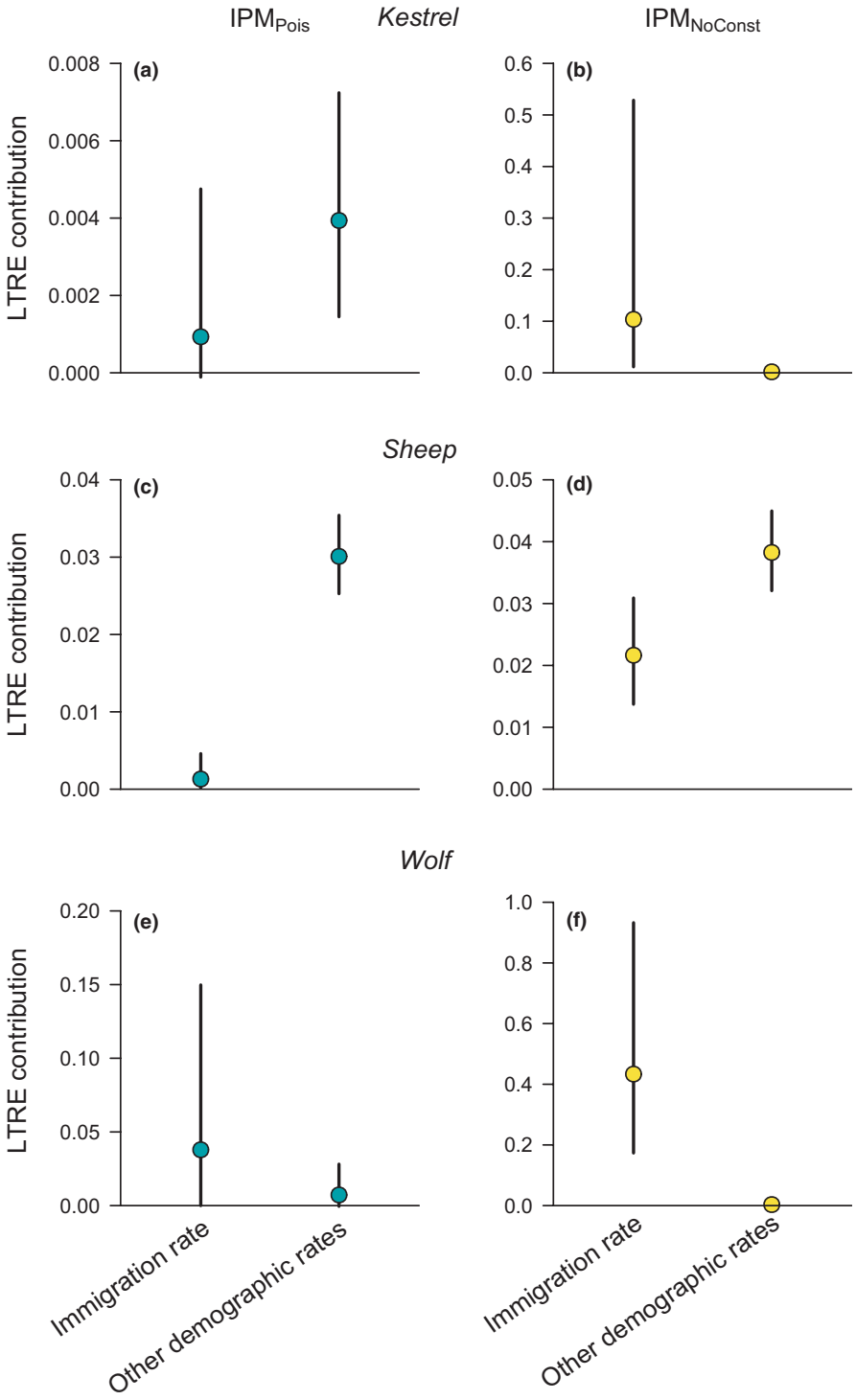

FIGURE 4 Transient LTRE contributions representing the part of variation in growth rate explained by immigration rate, and explained by the sum of all other demographic rates for the kestrel (a and b), the sheep (c and d) and the wolf (e and f) case study populations. Left panels represent estimates from the IPM_{Pois} parameterization, and right panels represent estimates from the $IPM_{noConst}$ parameterization. Dots show the posterior means, and lines show the 95% credible intervals

as the real datasets based on the estimated demographic parameters but where immigration (or any parameter of interest) is fixed in time. Then run the IPM using these simulated datasets and compare the contribution obtained with the one obtained when using the real dataset of interest. We provide a step-by-step procedure and R script on how to do so in Appendix 6. As an illustration, using data from a northern wheatear population, our procedure highlights that although immigration is estimated to be by far the main contributor of changes in population growth, a highly similar contribution would have been estimated in absence of any variation in the number of immigrants (Appendix 6). Because the inclusion of an *additional* parameter in IPMs can help prevent bias in the estimation of the other parameters (Riecke et al., 2019), it could be the case likewise regarding its temporal variation. Therefore, comparing estimates obtained with and without temporal variation in this *additional* parameter may be useful for better-informed inference regarding the other demographic parameters. That being said, we recommend not interpreting the contribution of *additional* parameters biologically

if the above-mentioned procedure does not suggest otherwise. Calling such a parameter an '*additional* parameter' throughout the text (and define it as immigration + bias in cases where this parameter describes immigration) may help prevent systematic biological misinterpretation.

An application of our results of practical conservation importance is that an estimated high contribution of immigration (relative to local reproduction and survival) to variation in population growth does not necessarily mean that local conservation measures (supporting local reproduction or survival) are of little consequence. Yet this is sometimes how an estimated strong (mean) contribution of immigration is interpreted (e.g. Schaub et al., 2012; Schaub & Ullrich, 2020) with subsequent suggestions that supportive measures should be undertaken at larger spatial scales. Our results suggest that because the importance of immigration is likely greatly overestimated (see the northern wheatear example in Appendix 6), then local measures may well be more effective conservation tools despite high IPM estimates on the contribution of immigration indicating otherwise.

If the main aim of a study was to investigate the temporal contribution of immigration to changes in population growth rate, it is advisable to empirically collect and use explicit data on immigration. In rare situations, where all breeders in the population are monitored and all offspring are marked, immigration can be estimated as the number of unmarked animals recruited into the population (Link & Barker, 2005). In the cases where all subpopulations are monitored, immigration and emigration from and towards each subpopulation can be estimated using multi-state models (Seward et al., 2019). Moreover, additional data on individuals' locations can be used in spatially explicit IPMs to estimate individuals' movements and hence immigration and emigration (Chandler & Clark, 2014; Chandler et al., 2018; Paquet et al., 2020), although extrapolation to movements at a scale larger than the study area may be problematic. Spatially explicit IPMs also allow accounting for spatial autocorrelation of parameters, accommodate data collected at different scales and hence avoid bias due to scale mismatch when estimating immigration. Because IPMs offer the possibility of using different types of data into a single modelling framework, then other types of available data such as spatial and genetic data (Millon et al., 2019) should be included in IPMs for more informed estimations of immigration and its temporal variation.

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CONFLICT OF INTEREST

None.

AUTHORS' CONTRIBUTIONS

M.L. and T.P. conceived the idea in discussion with M.P., J.K., D.A. and P.F.; Ø.F., C.G.J., M.A.C.N., K.N., J.M.P., H.S., L.S., V.T., P.W., C.W. and M.Å. collected the data; J.K., M.P. and D.A. conceived the simulation study; M.P. analysed the data and performed the simulation study with help from J.K.; M.P. led the writing of the manuscript together with D.A., J.K. and M.L. All authors contributed to the drafts and gave final approval for submission.

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DATA AVAILABILITY STATEMENT

Data can be accessed on Dryad Digital Repository https://doi.org/10.5061/dryad.xd2547dh0 (Paquet et al., 2021).

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